

THE INFLORESCENCE AND FLOWER-FORM IN *POLYGONUM*, SUBGENUS *PERSICARIA*.

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THE inflorescence of the subgenus *Persicaria* consists typically of a series of fascicles of small pedicellate flowers disposed along a lengthened axis. Each fascicle is subtended by a characteristic, more or less obliquely turbinate structure, the ocreola. The single flowers are each enveloped in a bract resembling the ocreola, but often so diaphanous or so hidden within the ocreola as to escape observation. The ocreolae, and consequently the fascicles within them, are spirally arranged; in the younger stages closely appressed and imbricated, concealing the buds. Later the rhachis usually elongates somewhat, and the ocreolae, in the more loosely flowered species, become somewhat separated and plainly visible, being then usually rather herbaceous in texture. In the dense-flowered types they may be nearly or quite hidden by the developing flowers, being then usually thinly membranous, in color and texture resembling the ocreae, of which they may be considered a floral counterpart. Most commonly the intervals between the ocreolae are fairly uniform, but in some species, especially the more laxly flowered, the basal grouping may be irregular or interrupted.

The number of flowers within an ocreola varies from one or two to seven or eight; most commonly a median number is found. The succession of flowering of the inflorescence as a whole is from the base to apex. The flowers of each fascicle also mature in a succession which may take some days or even weeks for its completion; often the first to appear in a particular fascicle have matured and disappeared considerably before the last have appeared above the margin of the ocreola.

In most American floras the terms spike, raceme, or spike-like raceme are used in reference to the inflorescence of these plants. As to the first, the flowers are plainly not sessile, the pedicels in all cases being evident even on casual examination, and in some cases much exserted and exceeding the accrescent calyx in length. The term raceme is usually applied to a simple inflorescence. For this rather peculiar compound type of floral arrangement the somewhat unsatisfactory term of spiciform or spicate panicle is perhaps the most appropriate.

The flowers are extremely simple, consisting of a 5-cleft (in some species sometimes, or even typically, 4-cleft) calyx, on the base of which, surrounding the ovary, are borne from 5 to 8 stamens; if more than five, of two series, in maximum 5 and 3. The latter case is considered the typical number; lesser numbers arise by reduction of the inner of the two whorls. Alternating with the attachment of the filaments, and often placed somewhat lower than that level, are glandular nectaries, which vary considerably in their development, being usually reduced in the smaller and more inconspicuously flowered species, and much larger in the more showy types, some of which are rather important honey-plants. The lenticular or trigonal ovary is surmounted by a cleft style whose segments are equivalent in number to the angles of the ovary. Each segment ends in a capitate or sometimes clavate stigma.

Collectors who have particularly observed this group of plants may have noted that the majority of the flowers open but briefly or remain closed. Stamens and styles are usually included, or barely exerted. Closer observation usually reveals, especially in terminal and well-developed panicles, some scattered flowers which are widely open, with stamens much in evidence and style less noticeable. In herbarium sheets the majority of the still present flowers are closed and bear achenes, usually well developed, but among these remain some flowers still wholly or partially open, whose ovaries show no sign of developing into fruit. The first impression, in field or herbarium, is that the open flowers represent immature or accidentally unfertilized specimens. A closer scrutiny of both open and closed flowers in various stages of development indicates, however, that here are two classes of flowers, which, though rather similar macroscopically, are quite different in function.

The open-type flowers appear always to be smaller, and the later to develop, in the fascicle. Their anthers are well developed and fully polleniferous. The pistil in the bud and early flowering stages appears quite normal, but in comparison with the other type of flower is smaller, and seems rarely or never to develop into a perfect achene. Commonly the open flower drops soon after anthesis, which is nearly simultaneous with the unfolding of the sepals. Not infrequently, however, it remains long enough to indicate rather conclusively, by its general withered appearance and the persistence of adherent pollen on the stigma, that its retarded development is a matter of organization and not of chance.

The inner structures of the more abundant fertile flowers show somewhat more variability. The styles are typically well developed; in some cases with straight branches; in others with the members more or less curled, sometimes in a complete circle, whereby the stigmas are held, while the flower is closed, in immediate proximity to the anthers. The anthers show, in different specimens of the same species, and in different species, various degrees of development. Usually they produce a fair quantity of pollen, though never the profuse amounts characteristic of the open flowers. As anthesis occurs before, or simultaneously with, whatever opening of the calyx may occur here is clear evidence of cleistogamy. A further evidence may be found in the common experience of collectors that specimens of this group, collected apparently with flowers and achenes in all stages of maturity, will, upon drying (particularly if the process is somewhat delayed) present a very high per cent of mature achenes and few gradations (in the fertile flowers) between these and the bud stage.

In some cases no pollen at all can be found in the partially developed and shriveled anthers. Yet (except in the rather special conditions noted in the amphibious group and to be described in another paper) these are often fully fruitful. The common appearance of shrunken pollen on the persistent stigmas may be held to indicate that actual fertilization and not apogamy has taken place.

In some members of the group, then, are found, in their extremes at least, three distinct types of flowers—in the terminology of Kerner pseudo-hermaphrodite male, pseudo-hermaphrodite female, and cleistogamous. Ordinary propagation evidently takes place by means of the cleistogamous type. Occasional cross-fertilization, including whatever hybridization may take place, presumably occurs by means of the pseudo-hermaphrodite types. Meehan,¹ the only American observer who appears to have published on these floral variations in *Polygonum*, reports that insects frequently visit the pseudo-hermaphrodite male flowers, but never, according to his observation, the cleistogamous ones, though these often open after close-fertilization has occurred. This writer did not note the presence of the pseudo-hermaphrodite female flowers—which, indeed, are very rare, if occurring at all, in some species, e. g., *P. pensylvanicum*, although occurring much more commonly in others, such as *P. hydropiperoides*. The presence of considerable quantities of foreign pollen, as observed

¹ T. Meehan, *Dimorphism in Polygona*. Acad. Nat. Sci. Phila. Proc. 1889, 59–61.

by the present writer in many of the open-type flowers, may be taken to corroborate the evidence of insect visitation. Actual cross fertilization by this means cannot be said to be absolutely proven, depending as it does mainly on visitation of the rather rare flowers of the virtually pistillate types by an insect loaded with pollen from one of the other types. The close proximity of the small flowers of this group, the considerable development of nectaries, and the reputation of the plants as bee-pasturage, adds probability to this form of transfer. The pollen of the group cannot be considered as produced in sufficient amounts, or as of the requisite type, to render transfer over great distance by wind feasible. In the subgenus *Persicaria* we have a group whose members have produced no well-defined mechanism of fruit transportation. The comparatively heavy achenes drop close to the parent plant, resulting under suitable conditions in succeeding seasons, in dense masses of plants whose inflorescences are thrust into close proximity above the foliage. Anthers of the virtually staminate flowers are usually thrust prominently outward, if not actually exerted. The pollen is shed readily. Given the occurrence of virtually pistillate flowers on a nearby plant, fertilization by geitonogamy seems a simple and probable way of insuring the fruit development which, as before noted, is usually found in the pseudo-hermaphrodite female panicles.

The type of polymorphy especially characteristic of the amphibious *Persicarias* has long been known in Europe, but seems to have escaped notice in American floristic works. Typical descriptions of the plants which have passed as *Polygonum amphibium* L. and *P. Muhlenbergii* Wats. in this country indicate both as having stamens and styles exerted. This condition indeed exists, but it is not the invariable one. Polymorphy here takes the form of what is usually termed heterostyly, and the term will be used here, although as far as the amphibious members of the group are concerned, the actual differences of elongation chiefly concern the stamens. One form, the long-styled, has the style-divisions exerted, while the stamens are invisible in the nearly closed calyx. In the short-styled form the flowers open widely, and the style-branches also appear, but with and somewhat surpassing them are the ends of the filaments and the anthers. The actual difference in length between the styles of the two forms is less than would at first appear; the amount of exertion depends also on the length of the ovary, which in the short-styled form is much reduced

and only rarely develops into an achene. If such development occurs, the style usually elongates somewhat further after anthesis, and the conditions closely parallel the proterandry described by Mueller¹ for the European *P. Bistorta*. Usually the virtually staminate flowers are, like those described above for the more typical members of the genus, quite infertile. Together with this heterostyly goes, typically at any rate, the segregation of the two types of flowers on different plants.

In the bud-stage the two-parted styles of the long-styled flowers are curled within the bud with the stigmas outward. As the flower opens the styles straighten and protrude strongly from the perianth. The styles usually remain exserted, though somewhat recurved, in fruit. The stamens are reduced in varying degrees; the anthers are thin-walled; and, as compared with the other form, smaller and somewhat shrunken. At most they contain but a few grains of pollen. Often they are quite empty. In the amphibious group this condition is accompanied by a high percentage of infertility. The rather showy and close-packed flowers possess well developed nectaries. Insects are probably responsible for such cross-fertilization as takes place. The usual closure of the long-styled flowers must hinder the process. While in the flowering stage no morphological difference between the flowers of a virtually pistillate panicle is evident, it seems highly probable that there are other causes of the high degree of sterility which lie deeper than failure in the transfer of the pollen. In *P. amphibium* L. and its American representative, *P. natans* (Michx.) Eaton, terrestrial forms flower rarely and appear still more rarely fertile than the aquatic. Achenes of terrestrial forms found in herbarium-material are usually imperfectly developed; so much is this the case that immaturity cannot be held wholly responsible for it. As achenes fall soon after maturity, the appearance of herbarium-material often exaggerates the actual degree of infertility in these plants, but it is certainly far more general than that found in other American species. In *P. coccineum* Muhl., which is more completely adapted to the terrestrial habitat, the dry-land forms more frequently produce fertile achenes. As previously noted, the long-styled forms open more or less, but in the event of fertilization at least, evidently rather briefly. During the development of the achene it is closely invested by the accrescent calyx. At maturity this is still tightly closed,

¹ Herman Mueller, *Die Befruchtung der Blumen durch Insekten*, 175 (1873).

considerably exceeding the fruit; it must be a factor of considerable importance in keeping the heavy achene afloat in water-currents and thus increasing the distribution of the species. These plants, however, must depend chiefly for their propagation on the long running or, in aquatic states, semi-floating rhizomes, which extend themselves very rapidly under suitable conditions. The long, meagerly rooting aquatic stems easily break off under stress of storm, current, or other strain, and, floating away, root readily where they happen to come to rest. The extreme development of these organs of perennation as compared with that in other members of the subgenus which produce achenes in profusion suggests that here we have floral degeneration consequent upon perfection of vegetative means of reproduction. Certain other observations, to be touched upon in another paper, indicate the presence of still other factors, at least as regards the American species, and the matter can by no means be regarded as settled, nor of easy settlement.

In view of the well-known occurrence of this type of polymorphy in the European *Polygonum amphibium* L., and the considerable study that the group to which it belongs has received in this country, it seems the more remarkable that the phenomenon has so far escaped notice on this continent. It may be mentioned that the habit-drawings of the species most concerned in Small's Monograph¹ plainly show the long-styled forms. The text and the detail-drawings, however, indicate the exertion of both sets of essential organs. Some 45 American species of this group have been proposed by various writers who failed to note the development of two types of flowers on separate plants. Those not especially concerned with the multiplication of names will view this lack of observation with a certain degree of philosophy. Nieuwland, the principal present day exponent of the views of Greene² regarding this group, in a paper³ published subsequent to his extensive review of the American Polygonums⁴ sought to reduce *P. longistylum* Small to the problematical *P. bicornis* Raf. on the ground that the former alone in the American flora possesses exerted styles. *P. bicornis* will be dealt with more at length

¹ Small, *Monograph of the North American Species of the Genus Polygonum*. Mem. Dept. Bot. Columb. Col. i. (1895).

² E. L. Greene, *Certain Polygonaceous Genera*. Leaflets of Bot. Obs. and Crit. i. 17-50 (1904).

³ Nieuwland, *Polygonum longistylum* Small, a synonym. Am. Midl. Nat. iii. 200, 201 (1914).

⁴ Nieuwland, *Our amphibious Persicarias*, Am. Midl. Nat. ii. 1-24. 200-247 (1911-12).

in another paper dealing primarily with the systematic standing of *P. longistylum* Small and its close relatives.

P. longistylum, originally described from the long-styled form alone, was reported by Robinson¹ as heterostyl, and the fact also noted by that author and Fernald in the seventh edition of Gray's Manual. In contradistinction to the conditions in the amphibious group, the style in *P. longistylum* is definitely reduced in the short-styled form. Here, also, short-styled forms tend to sterility, but the percentage of barrenness is by no means so great as that which obtains in the amphibious group. Usually a short-styled panicle will produce at least a few apparently normal fruits. Here, as in the amphibious group, the flower-types are segregated, or virtually so, so that the condition is practically a dioecious one. A perennial plant described as new in another paper in this series displays the same type of heterostyly.

It is of interest to observe that in *Polygonum pensylvanicum*, closely related to *P. longistylum*, and still more in *P. mexicanum*, of the same group, a trend toward heterostyly may often be observed, but, so far as noted by the writer in the examination of a considerable amount of material, it does not reach the point of segregation of types, nor does there appear to be any great variation among plants in percentage of sterility.

It is highly probable that a study of the flower-form of members of the subgenus *Persicaria* in other sections of the world will bring to light other cases of heterostyly.

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PROPER USE OF THE NAME LEONTODON.

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THE English name dandelion, the French name dent-de-lion, and the Latin names *dens-leonis* and *leontodon* all mean exactly the same thing and have the same derivation. As stated by Tournefort in 1719 (Instit. 469). "Dens leonis à foliorum formâ, quae Leonis maxillam dentibus suis instructam aemulari existimatur."

Tournefort treated the dandelions and related plants under the generic name *Dens leonis*. Linnaeus rejected double headed generic

¹ Robinson, *Notes on some Polygonums of western North America*. Proc. Bost. Soc. Nat. Hist. xxxi. 265 (1904).